

Competition between *Erica tetralix* L. and *Molinia caerulea* (L.) Moench as affected by the availability of nutrients

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SUMMARY

An experiment was conducted to study the effects of nutrient addition and changes in ground-water level on competition between *Erica tetralix* L. and *Molinia caerulea* (L.) Moench. The growth and mortality of *Erica* in mixtures with *Molinia* was compared with that in monocultures. The experiment included four nutrient treatments (unfertilized, fertilized with 15 g N m⁻², 30 g N m⁻², or 3.3 g P m⁻²) and three watertable depths (0, 20 or 40 cm below soil surface) in a factorial combination of twelve series. In the unfertilized series with a waterlevel at 20 cm below the soil surface there was no difference between the growth of *Erica* in monoculture and that in mixture. Adding phosphate or lowering the waterlevel to 40 cm below the soil surface led to a significant negative effect of competition by *Molinia* on the growth of *Erica*. In only one of the treatments fertilized with nitrogen was the growth of *Erica* negatively affected by *Molinia*. At the highest groundwater level there was a strong reduction in growth and nutrient absorption by *Erica* and a strong increase in mortality of first year shoots. It is suggested that *Erica* is crowded out by *Molinia* after an increase in the nutrient availability or an improvement of aeration. Extremely nutrient-poor, water-logged sites have probably to be considered to be refuges for *Erica*, where it does not show its optimum growth. The results point to a positive interaction between nitrogen and phosphorus availability for uptake by plants.

KEY-WORDS: *Erica* - *Molinia* - Competition - Nutrients - Water-table.

RÉSUMÉ

Une étude expérimentale a été réalisée en vue d'étudier les effets d'un apport d'éléments nutritifs et d'une modification du niveau de la nappe phréatique sur la compétition entre *Erica tetralix* L. et *Molinia caerulea* (L.) Moench. La croissance et la mortalité d'*Erica* cultivé en mélange avec *Molinia* ont été comparées avec les résultats observés en monoculture. L'expérience comprenait quatre niveaux d'alimentation en éléments minéraux (témoin non fertilisé, et trois traitements fertilisés : 15 g N m⁻², 30 g N m⁻², 3,3 g P m⁻²) ainsi que trois profondeurs de la nappe phréatique (0, 20 ou 40 cm au-dessous de la surface du sol) et a été réalisé selon un plan factoriel portant sur douze combinaisons. Dans le cas du témoin non fertilisé combiné avec une profondeur de nappe de 20 cm, il n'y a eu chez *Erica* aucune différence de croissance entre la culture pure et la culture mixte. Un apport de phosphate, de même que le fait d'abaisser le niveau de la nappe à 40 cm de profondeur, ont entraîné un effet compétitif négatif sur la croissance d'*Erica* en présence de *Molinia*. Le même effet a été observé dans le cas d'un apport d'azote, mais pour une seule combinaison. Lorsque le niveau de la nappe affleure, on observe chez *Erica* une forte réduction de sa croissance et de l'absorption d'éléments minéraux, ainsi qu'une forte augmentation du taux de mortalité des pousses de première année. Ceci suggère la possibilité selon laquelle *Erica* est éliminé par *Molinia* aussi bien dans le cas d'un accroissement de la fertilité du sol que dans celui d'une amélioration des conditions d'aération du sol. Les milieux extrêmement pauvres sur le plan de la disponibilité en éléments nutritifs et saturés en eau doivent probablement être considérés comme des refuges pour *Erica*, qui n'y atteint pas sa croissance maxi-

male. Les résultats indiquent en outre une interaction positive entre la disponibilité de l'azote et celle du phosphore par rapport à l'absorption de ces éléments par les plantes.

MOTS-CLÉS : *Erica* - *Molinia* - *Compétition* - *Éléments nutritifs* - *Nappe phréatique*.

INTRODUCTION

Wet heathland communities in the Netherlands are typically dominated by *Erica tetralix* L. Other plant species that occur less frequently in these communities are: *Scirpus caespitosus* L., *Gentiana pneumonanthe* L., *Drosera intermedia* Hayne and *Lycopodium inundatum* L. During the last few decades there has been a large increase of *Molinia caerulea* (L.) Moench in wet heathlands in a large number of localities in the Netherlands. On many sites this process has led to stands of *Molinia* in which no other plant species occur. It is not yet known what has caused this important change in the species composition of these communities, but there have been a number of changes in the external environment of these ecosystems which could be responsible:

1. Grazing by sheep of most heathlands ended in the beginning of this century. This has led to a decrease in the export of nutrients from these ecosystems, but has also constituted the end of selective removal of *Molinia* by sheep.
2. The mean water-table depth of most wet heathlands has been lowered to favour nearby agricultural practices.
3. Since most wet heathlands are embedded in mainly agricultural landscapes, the large increase in the use of fertilizers may have caused a higher input of nutrients into heathland ecosystems by air or groundwater nutrient transport.
4. Since the 1950's there has been an increase in acidity and in concentrations of nitrogen and sulphur oxides in rain water (HUTCHINSON & HAVAS, 1980).

Since each of these changes in the Dutch landscape may, amongst others, have led to an increase in the availability of nutrients for uptake by plants, we will focus in this article on the effects of changes in nutrient availability on the occurrence of *Erica* and *Molinia*.

In Great Britain *Erica* occurs most frequently on sites with extremely low concentrations of nitrogen and phosphorus in the soil and a high water table, whereas *Molinia* dominates on sites with a higher nutrient availability and a lower water table (RUTTER, 1955; LOACH, 1966). WEBSTER (1962) found a positive correlation between carbon dioxide and hydrogen sulphide concentrations in soil water and the cover percentages of *Erica*, whereas the cover of *Molinia* showed a negative correlation. In contrast with these observations, LOACH (1968) observed that *Erica* seedlings transplanted to plots cleared of original vegetation, showed higher growth on relatively nutrient-rich, well-aerated sites. Furthermore, under laboratory conditions *Erica* appeared to be more sensitive to high carbon dioxide and hydrogen sulphide concentrations than *Molinia* was. The contradiction between the results from correlative studies in natural vegetation and those from experiments in field and laboratory may be caused by competition between *Erica* and *Molinia*. It has been shown that the availability of nutrients can have important effects on the competitive relationship between different plant species (BERENDSE, 1981; 1982; 1983).

Our hypothesis is that *Erica* disappears from nutrient-rich, well aerated sites because of competition with *Molinia*, whereas on extremely poor, water-logged sites *Erica* can survive, because here the competitive ability of *Molinia* is greatly reduced. According to this view, the increase of *Molinia* in wet heathlands in the Netherlands

is caused by an increase in nutrient availability. The mechanism of such an increase will be discussed elsewhere (BERENDSE, in prep.). In order to test our hypothesis we carried out an experiment to study the effect of the addition of nitrogen or phosphate on competition between the two species. Because of possible interference between watertable depth and nutrient availability, the influence of different groundwater levels was included in this experiment as well.

MATERIAL AND METHODS

In order to simulate the natural growing conditions as closely as possible, we started our competition experiment with sods cut from natural heathland. The sods were cut in the wet heathland area Kruislaarse heide, located in the central part of the Netherlands (52° 13' N, 5° 32' E). A large part of this area is nowadays dominated by *Molinia caerulea* (L.) Moench, whereas other parts still are dominated by *Erica tetralix* L. The vegetation in these areas is a typical *Ericetum tetralicis* (WESTHOFF & DEN HELD, 1969). Other plant species occurring in these parts, are: *Gentiana pneumonanthe* L., *Scirpus caespitosus* L. and *Calluna vulgaris* (L.) Hull. In moist places small patches of *Lycopodium-Rhynchosporium albo-fuscae* communities (WESTHOFF & DEN HELD, 1969) occur. The water table in the area fluctuates from 1.4 m below to a few centimeters above the soil surface. The soil consists of fine sand and is strongly podzolized. On top of the soil profile is an organic matter layer about 8 to 10 cm deep. Nitrogen and phosphorus are almost exclusively restricted to this upper layer. The ammonium concentration in this layer varies between 3.3 and 18.9 mg ammonium nitrogen kg⁻¹ dry soil. The concentrations of nitrate in the soil are always very low (< 0.2 mg nitrate nitrogen kg⁻¹ dry soil). The soil in the upper layer contains 3.2 to 6.1 mg phosphate kg⁻¹ dry soil (2 g dry soil extracted with 120 ml water). The pH (H₂O) varies between 3.8 and 4.5.

On 18 April 1981, when growth of the two species had not yet started, sods were cut in 30 by 30 cm sections to a depth of about 10 cm. These sods were covered with *Erica* and *Molinia* and included no other plant species. The relative cover of *Erica* and *Molinia* on this site was in August 1981 55.5 % and 44.5 %, respectively. The sods were transported to an experimental field and placed in plastic containers with an area of 30 by 30 cm and a height of 50 cm. These containers were filled with fine glacial sand to about 10 cm from the rim and the sods were placed on top of the sand. In 60 sods we created monocultures of *Erica* by removing the *Molinia* plants. The shoots of *Molinia* were pulled from the sods together with a part of their roots. The biomass that was removed from the sods in this way was generally not more than 5 % of the total amount of biomass on the sod. In another 60 sods *Molinia* was not removed.

The experiment included three watertable depths and four different nutrient applications in a factorial combination of twelve treatments. The three watertable depths were: 0 cm (H), 20 cm (IM) and 40 cm (L) below soil surface. The watertable depths in the IM and the H series were maintained by holes in the containers at 20 or 40 cm below the rim. The nutrient treatments were as follows: an unfertilized control receiving only tapwater (O); 15 g nitrogen m⁻² (1 N); 30 g nitrogen m⁻² (2 N); 3.3 g phosphorus m⁻² (P). The nitrogen was given as an ammonium nitrate solution, the phosphorus as a sodium phosphate solution. From 15 May to 1 September each container in the fertilized series received 1 l of nutrient solution three times a week. The unfertilized series received equal amounts of tapwater. During dry periods the containers were supplied with additional tapwater to maintain the water tables. The tapwater contained 0.9 mg N l⁻¹ and 0.03 mg P l⁻¹. The amounts of phosphorus and nitrogen supplied to the unfertilized sods by tapwater were respectively about 1 % of the amount of phosphorus applied to the P series and 6 % and 3 % of the amounts of nitrogen applied to the 1 N and 2 N series. Each treatment of the monoculture and the mixture series was replicated five times. The experiment was divided into five blocks with monocultures and five blocks with mixtures. The blocks were arranged alternately. The complete experiment included: 12 treatment × 2 types of stands × 5 replicates = 120 containers.

On 9 and 10 September the sods were removed from the containers and taken into the laboratory. The above ground plant biomass was harvested by clipping at the soil surface. We distinguished between the following components: living first-year shoots of *Erica* (P); dead first-year shoots of

Erica (*D*); shoots and stems of *Erica* grown in previous years (*B*); living-shoots of *Molinia*; and dead shoots of *Molinia*. The harvested biomass was dried for 48 hours at 70° C and weighed. After drying, the plant material of the replicates was bulked and ground for nutrient analysis. The concentration of total nitrogen was determined volumetrically in samples of 2 mg ground material. Samples of 125 mg were ashed for 5 hours at 550° C and digested in 5 ml 3 *N* hydrochloric acid, after which 95 ml distilled water was added. Phosphorus in this solution was determined colorimetrically by means of an auto-analyzer after reduction to phosphomolybdenum blue.

RESULTS

Dry matter production of Erica tetralix

For each container we calculated the ratio between the living biomass grown during the experimental period (*P*) and the biomass grown during the previous years (*B*) (table I). This ratio can be considered to be an approximation of the relative growth rate during the experimental period. We applied a logarithmic transformation to these ratios, prior to statistical analysis. In the *Erica* monocultures at a watertable depth of - 20 cm the application of phosphate or nitrogen leads to a higher *P:B* ratio, although the difference is not statistically significant (using a *t*-test). Lowering the watertable from - 20 cm to - 40 cm leads, in the unfertilized and the phosphate fertilized series, to an increase and, in the nitrogen fertilized series, to a decrease of productivity. In the treatments with the high watertable the *P:B* ratio is clearly reduced relative to the *P:B* ratios in the other series. In all four nutrient treatments this reduction of the productivity is highly significant ($P < 0.0005$).

TABLE I. — The ratio between the dry weight of the first year shoots grown during the experimental period (*P*) and that of the biomass grown during previous years (*B*) of *Erica tetralix* L. in monoculture and in mixture with *Molinia caerulea* (L.) Moench.

<i>Monocultures</i>				
Nutrient treatment Water-table	<i>P</i>	<i>O</i>	1 <i>N</i>	2 <i>N</i>
0 cm	0.008	0.022	0.006	0.003
- 20 cm	0.962	0.638	0.992	1.063
- 40 cm	1.179	0.880	0.724	0.942
<i>Mixtures</i>				
Nutrient treatment Water-table	<i>P</i>	<i>O</i>	1 <i>N</i>	2 <i>N</i>
0 cm	0.028	0.113	0.106	0.117
- 20 cm	0.503	0.564	0.647	0.477
- 40 cm	0.225	0.429	0.366	0.551

In the mixtures with a watertable of - 20 cm, fertilization with nitrogen or phosphorus does not cause an increase of the *P:B* ratio in contrast to the response in the monocultures. In the series with a watertable at - 40 cm the productivity is, in three of the four nutrient treatments, reduced relative to those in the series with a watertable at - 20 cm. Also in the mixtures the *P:B* ratios in the inundated series

are clearly below the ratios in the two other series (0: $P < 0.05$; P : $P < 0.01$; $1N$: $P < 0.005$; $2N$: $P < 0.05$).

In order to compare the productivity of *Erica* in monoculture and that in mixture we introduced the competition coefficient of *Erica* with respect to *Molinia*:

$$c_{em} = \frac{(P/B)_{\text{mixt}}}{(P/B)_{\text{mono}}}$$

If the competition coefficient exceeds unity the growth of *Erica* is more negatively influenced by intraspecific competition than by competition exerted by *Molinia*. If the competition coefficient is below unity, the growth of *Erica* is more negatively affected by *Molinia* plants than by competition between *Erica* plants. The logarithmically transformed values of the competition coefficient are presented in figure 1. For each treatment the deviation from unity was tested by comparing the logarithmically transformed values of the $P:B$ ratios in mixture with those in monoculture. In the unfertilized series with a watertable of -20 cm the deviation from unity is very small and not significant. At this watertable depth the competition coefficient is signi-

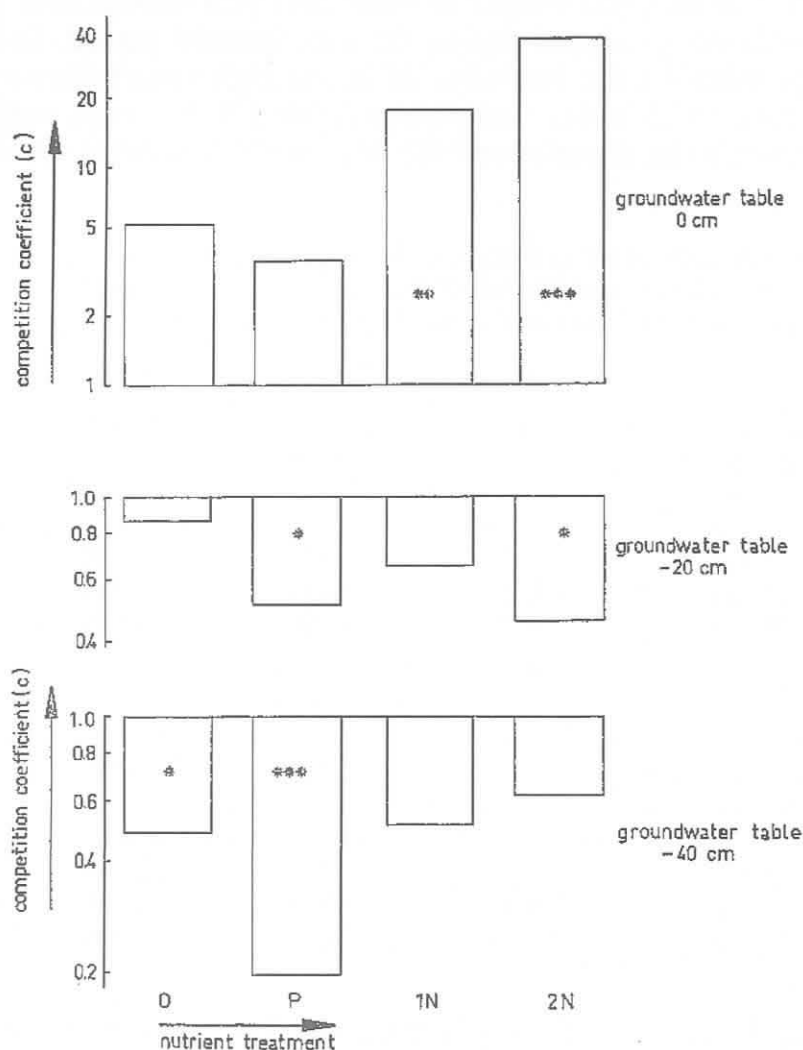


FIG. 1. — The competition coefficient of *Erica tetralix* L. with respect to *Molinia caerulea* (L.) Moench (c_{em}). Note logarithmic scale of y-axis. See text for further explanation.

ificantly below unity in the *P*- and the 2*N*-treatment ($P < 0.05$). In the series with a watertable depth of -40 cm the competition coefficient is also in the unfertilized treatment significantly below unity ($P < 0.05$). In the *P*-treatment there is a strong reduction of the competition coefficient ($P < 0.005$). In the two nitrogen treatments at this watertable no significant deviations from unity were found. In the inundated treatments the competition coefficient clearly exceeds unity in contrast to that in the treatments with lower watertables. In the two inundated nitrogen treatments the deviation from unity is significant ($P < 0.01$). Here the growth of *Erica* seems to be positively influenced by the presence of *Molinia*.

Mortality of Erica tetralix

During the experiment we observed that a high percentage of first year shoots, that died, remained attached to the plant until the end of the experimental period. We calculated the relative mortality of first year shoots by:

$$M = \frac{D}{P + D}$$

i. e. the ratio between the weight of dead first year shoots and the total weight of the first year shoots produced during the experimental period. In both the monocultures and the mixtures the mortality *M* in the high-watertable series is much higher than in the series with lower watertables (table II). For each nutrient treatment the difference between the *H*-series and the *IM*- or the *L*-series is significant ($P < 0.005$).

TABLE II. — *The mortality of Erica tetralix L. in monoculture and mixture. The mortality is calculated by the ratio between dry weight of dead first year shoots at the end of the experimental period (D) and total dry weight of dead and living first year shoots at that time.*

<i>Monocultures</i>				
Nutrient treatment Water-table	<i>P</i>	<i>O</i>	1 <i>N</i>	2 <i>N</i>
0 cm	0.621	0.374	0.610	0.909
— 20 cm	0.018	0.014	0.013	0.025
— 40 cm	0.009	0.020	0.025	0.021
<i>Mixtures</i>				
Nutrient treatment Water-table	<i>P</i>	<i>O</i>	1 <i>N</i>	2 <i>N</i>
0 cm	0.266	0.214	0.245	0.191
— 20 cm	0.013	0.010	0.018	0.014
— 40 cm	0.023	0.038	0.026	0.008

In the monocultures the mortality in the three fertilized treatments is clearly, but not significantly, higher than the mortality in the unfertilized series. In all nutrient treatments the mortality in the monocultures is higher than that in the mixtures. This difference is only significant in the 2*N*-treatment ($P < 0.05$).

Nitrogen and phosphorus uptake by Erica tetralix and Molinia caerulea

Nitrogen concentrations in the two nitrogen fertilized series are generally slightly higher than in the unfertilized and the phosphorus fertilized series (table III). In the series with a high groundwater level the nitrogen concentrations in the P-treatment exceeded also those in the unfertilized treatment. The phosphorus concentration in the P-treatments is in each series clearly higher than that in the unfertilized treatment (table IV). The phosphorus concentrations in the nitrogen fertilized treatments exceed those in the unfertilized treatments as well in *Molinia*, and in *Erica* in mixture at the intermediate groundwater level.

TABLE III. — Nitrogen concentrations (mg N g⁻¹) in first year shoots of *Erica tetralix* L. grown during the experimental period in monoculture and in mixture with *Molinia caerulea* (L.) Moench and in *Molinia* shoots grown during the experimental period in mixture with *Erica tetralix* L.

Erica tetralix in monoculture				
Nutrient treatment Water-table	P	O	1N	2N
0 cm	11.5	10.9	15.0	13.3
— 20 cm	13.8	13.9	15.4	15.7
— 40 cm	14.4	13.9	13.9	15.6
Erica tetralix in mixture				
Nutrient treatment Water-table	P	O	1N	2N
0 cm	11.3	10.7	14.1	11.4
— 20 cm	11.4	11.5	13.8	14.9
— 40 cm	13.4	12.5	12.7	14.5
Molinia caerulea in mixture				
Nutrient treatment Water-table	P	O	1N	2N
0 cm	18.1	12.7	14.6	12.7
— 20 cm	9.8	10.9	13.9	15.4
— 40 cm	10.9	11.4	11.5	17.6

We multiplied the nitrogen and phosphorus concentration in the first year shoots of *Erica* and in the shoots of *Molinia* with the dry weight of these plant parts at the end of the experimental period. In this way we obtained a value for the amount of nitrogen and phosphorus in the plant parts grown during the experimental period. This amount originates from uptake by plants roots and from translocation of nutrients from other plant parts. Moreover, part of the nutrients taken up will be invested in other plant parts such as roots and stems, but we considered the amount of nutrients present in the newly grown plant parts, at the end of the experimental period, to be positively correlated to the total uptake of nutrients. At the high water level the uptake

TABLE IV. — Phosphorus concentrations (mg P g⁻¹) in first year shoots of *Erica tetralix* L. grown during the experimental period in monoculture and in mixture with *Molinia caerulea* (L.) Moench and in *Molinia* shoots grown during the experimental period in mixture with *Erica tetralix* L.

Erica tetralix in monoculture				
Nutrient treatment Water-table	P	O	1N	2N
0 cm	1.46	0.67	0.64	0.53
— 20 cm	1.13	0.40	0.30	0.45
— 40 cm	1.19	0.57	0.50	0.53
Erica tetralix in mixture				
Nutrient treatment Water-table	P	O	1N	2N
0 cm	0.59	0.51	0.32	0.33
— 20 cm	0.66	0.28	0.52	0.51
— 40 cm	0.60	0.40	0.49	0.32
Molinia caerulea in mixture				
Nutrient treatment Water-table	P	O	1N	2N
0 cm	2.17	0.16	0.58	0.40
— 20 cm	0.71	0.18	0.58	0.23
— 40 cm	0.46	0.21	0.38	0.37

of nitrogen by the first year shoots of *Erica* is extremely low in contrast to the uptake of nitrogen by the *Molinia* shoots (fig. 2). In the series with a watertable depth of — 20 or — 40 cm the amounts of nitrogen taken up are higher both in the nitrogen and the phosphorus fertilized series than in the unfertilized series. Also phosphorus uptake by *Erica* at high water levels is extremely low (fig. 3), while phosphorus uptake by *Molinia* is not strongly reduced. In the *Erica* monocultures does the phosphorus uptake at the lowest groundwater table exceed that at the intermediate water table. At all water levels phosphorus uptake in mixtures is higher both in the nitrogen and the phosphorus fertilized series than in the unfertilized series. This phenomenon points to a possible interaction between the availability of nitrogen and phosphorus.

DISCUSSION

LOACH (1968) transplanted *Erica* seedlings to nutrient-poor sites with a high groundwater level and to relatively nutrient-rich sites which were well-aerated. The seedlings were planted in plots cleared of standing vegetation to prevent interspecific competition. Surprisingly, *Erica* showed the highest growth rate on the nutrient-rich sites, whereas in natural, undisturbed situations its highest abundance occurs on extremely poor sites (RUTTER, 1955; LOACH, 1966). In our experiment we observed that the addition of nutrients increased the growth rate of *Erica* in monoculture.

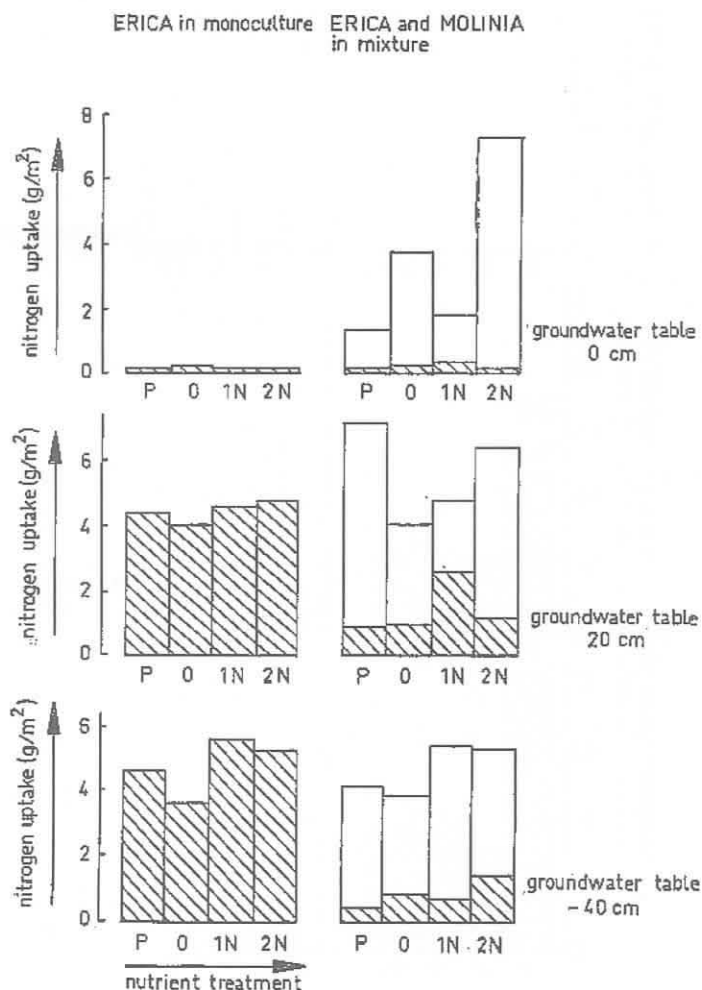


FIG. 2. — The amount of nitrogen of first year shoots of *Erica tetralix* L. (shaded area) and that in the above ground biomass of *Molinia caerulea* (L.) Moench (white area) in monoculture and in mixture.

From comparisons between the productivity of *Erica* in monoculture and mixture in the series with an intermediate water level, we conclude that the addition of nutrients changes competition between *Erica* and *Molinia*. In the containers with *Molinia* *Erica* showed, in a number of nutrient treatments, significantly lower productivity than in containers without *Molinia*. This effect is especially clear in the treatments fertilized with phosphate. This phenomenon was observed in only one nitrogen treatment. Nitrogen fertilization did not affect competition in the series with the lowest water level possibly because an important fraction of the supplied nitrogen was leached. Lowering the water table from -20 to -40 cm had the same effect as adding phosphorus. The amount of nutrients in the newly grown plant parts indicate, however, that lowering the water level does not lead to an increased availability of one of the nutrients. SHEIKH (1969), when studying competition between *Erica* and *Molinia*, found that the application of a nutrient solution led to a strongly reduced survival of *Erica*. In his experiment the effect of nutrient addition completely masked the possible effect of competition by *Molinia*. Even in the highest nitrogen treatment we applied each time an amount of nutrients that was only 10-20 % of that SHEIKH (1969) applied at each fertilization. This higher nutrient application at

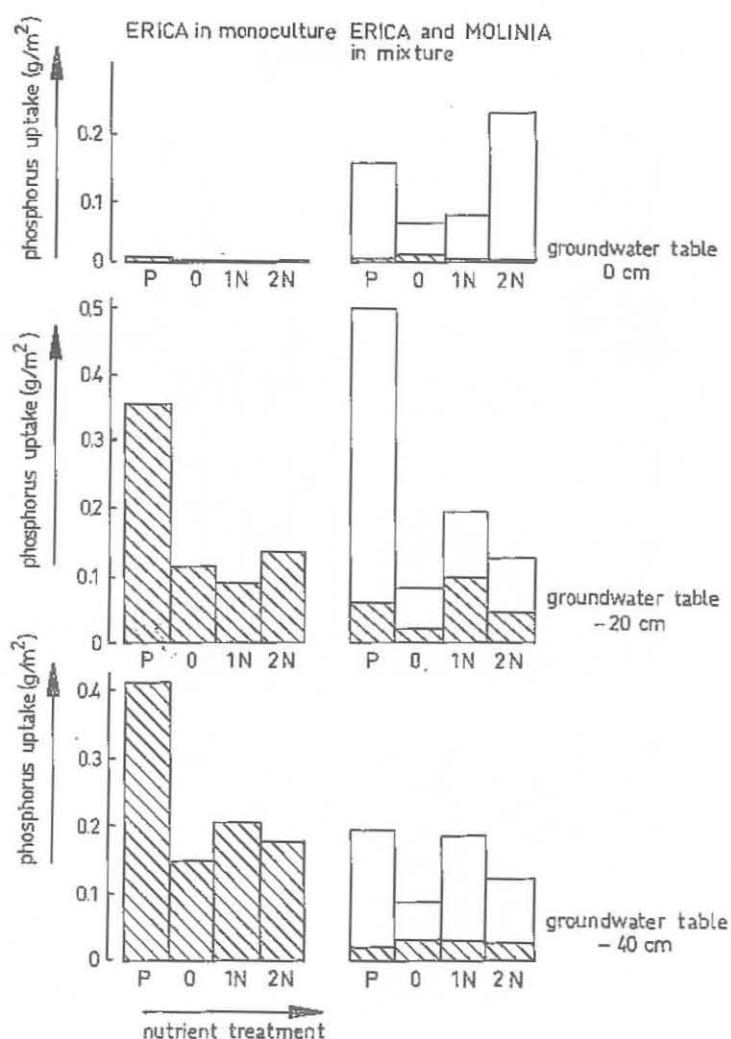


FIG. 3. — The amount of phosphorus in first year shoots of *Erica tetralix* L. (shaded area) and that in the above ground biomass of *Molinia caerulea* (L.) Moench (white area) in monoculture and in mixture.

each fertilization and the use of seedlings instead of adult plants may have caused osmotic damage to the plants. This was avoided in our experiment, except possibly in the inundated series in which an accumulation of nutrients in the soil solution may have taken place. In fertilized plots SHEIKH (1969) found a significant negative effect of competition by *Molinia* on sites which are normally dominated by *Molinia*, while on sites normally dominated by *Erica* such an effect was not demonstrated.

In our experiment we found that growth of *Erica* was dramatically reduced and mortality greatly increased in the series where the water level was at the soil surface. Nutrient absorption by *Erica* was greatly reduced in this series compared to nutrient absorption by *Molinia*. This suggests that not the availability of nutrients was reduced at the highest water level, but that the ability of *Erica* to absorb nutrients was reduced. This view is supported by the observation that the application of nutrients to the *Erica* monocultures in the inundated series does not lead to enhanced nutrient uptake. In mixtures growing together with *Molinia*, *Erica* exhibited increased growth and lower mortality than in the monocultures. On warm and sunny days *Molinia* showed such high transpiration that the water level in the mixtures was lowered 1 or 2 cm below the soil surface before additional water was supplied. These short periods

of aeration, which did not occur in the monocultures, may explain the better growth of *Erica* in mixture. SHEIKH (1970) observed that *Erica* was less resistant to high concentrations of carbon dioxide and hydrogen sulphide than *Molinia* was. This difference between the two species may have caused the difference in nutrient uptake in the inundated containers. Probably *Erica* is adapted to soils with a high ground-water level by its ability to form a shallow rooting system that avoids the part of the soil that is oxygen-deficient (RUTTER, 1955; SHEIKH & RUTTER, 1969). *Molinia*, on the other hand, has intercellular spaces in its roots that are lysigenous in origin (SHEIKH & RUTTER, 1969). WEBSTER (1962) showed that these cortical air spaces contain, even under extremely oxygen-deficient conditions, air with an oxygen percentage of at least 15 %. Oxygen transport through intercellular spaces in its roots, may allow *Molinia* to absorb nutrients under inundated conditions.

It seems that *Erica* dominates extremely nutrient-poor, water-logged sites, because the competitive ability of *Molinia* is reduced there. On sites with higher nutrient availability and better aeration the competitive ability of *Molinia* is sufficiently high to have negative effects on the growth of *Erica*. The sites where *Erica* most frequently occurs and where it does not experience optimum growth have to be considered refuges for this species. On the basis of our results we may expect that a possibly increased nutrient availability in wet heathland ecosystems in the Netherlands may have led to an increase of *Molinia* and a decline of *Erica*.

The phosphorus uptake at the two lower water levels was not only stimulated by the application of phosphate, but also by the supply of nitrogen. We found the same phenomenon for the uptake of nitrogen. Since nutrient analysis was not carried out in material of separate replicates, conclusions from these results are speculative; however, since the described pattern occurs in most series, it seems there is an interaction between the availability of nitrogen and phosphorus. Such a positive interaction has been demonstrated by other authors as well (BLACK, 1968; MUNEVAR & WOLLUM, 1977; ROSS & BRIDGER, 1978). This mutual influence may be caused by a positive response of root growth to the supply of nitrogen or phosphate, thus increasing root absorption of the other nutrient. Another possible explanation is that fertilization stimulates microbial activity and causes thereby an enhanced mineralization rate of nitrogen and phosphorus (BERENDSE & BOSATTA, in manuscript). A more detailed knowledge of these possible interactions between nitrogen and phosphorus cycling may be important to our understanding of the effects of changes in nutrient inputs into nutrient-poor ecosystems.

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